

PHYTOLITH EVIDENCE FOR THE LACK OF A GRASS UNDERSTORY IN A
SEQUIADENDRON GIGANTEUM (TAXODIACEAE) STAND IN THE CENTRAL
SIERRA NEVADA, CALIFORNIA

RAND R. EVETT

Division of Ecosystem Science, Department of Environmental Science, Policy,
and Management, University of California, Berkeley, CA 94720-3110
revett@sonic.net

ROY A. WOODWARD¹

California Department of Parks and Recreation, Sacramento, CA 95814

WAYNE HARRISON

California Department of Parks and Recreation, Calaveras Big Trees State Park,
Arnold, CA 95223-0120

JAMES SUERO

California Department of Parks and Recreation, Sacramento, CA 95814

PATRICIA RAGGIO

California Department of Parks and Recreation, Calaveras Big Trees State Park,
Arnold, CA 95223-0120

JAMES W. BARTOLOME

Division of Ecosystem Science, Department of Environmental Science, Policy,
and Management, University of California, Berkeley, CA 94720-3110

ABSTRACT

Tree ring fire-scars in *Sequoiadendron giganteum* (giant sequoia) stands record a high frequency, low intensity, prehistoric fire regime. Difficulties achieving short prehistoric fire return intervals with prescribed burns at a *S. giganteum* stand in Calaveras Big Trees State Park, California, currently characterized by dense tree cover with little understory vegetation due to over a century of fire suppression, suggest that a prehistoric grass understory provided fine fuel required for frequent fire spread. We used phytolith analysis to test this hypothesis. Phytoliths, microscopic silica bodies found in many plants but produced in large quantities with distinctive morphotypes in grasses, are preserved for thousands of years in the soil. Soils under vegetation with extensive prehistoric grass cover retain a high concentration of grass phytoliths regardless of historic vegetation changes. Phytoliths were extracted from soil samples taken from pits dug at 14 plots throughout a *S. giganteum* stand in the South Grove Natural Preserve. Soil phytolith weight for most plots, currently without grass cover and comprising most of the stand, was less than 0.10%, consistent with reported values for forests with no grass in the understory. Soil phytolith weights for ridge-top plots and plots near the stream channel were significantly higher, suggesting localized areas with sparse grass cover. The hypothesis that there was substantial prehistoric grass cover in this *S. giganteum* stand was rejected.

Key Words: *Sequoiadendron giganteum*, giant sequoia, phytoliths, fire regime, California grasses, California paleoecology, Sierra Nevada, Calaveras Big Trees.

Fire is an important ecosystem process in *Sequoiadendron giganteum* (Lindley) Buchholz (giant sequoia) stands in the central Sierra Nevada in California. *Sequoia giganteum* appears to be dependent upon ground fires for regeneration in many areas. Cones open following fire to release seeds; a few years following ground fire, newly germinated *S. giganteum* seedlings dominate burned areas (Kilgore 1973; Parsons and

DeBenedetti 1979; Mutch and Swetnam 1995). Analyses of tree-ring fire-scars from living trees and stumps in the Sierra Nevada indicate that prior to the mid-1800s there was a composite mean fire return interval of approximately five years in *S. giganteum* stands of the mixed-conifer forest type (Swetnam 1993; Caprio and Swetnam 1995; Parsons 1995). This means that tree-ring fire-scars recorded a surface fire somewhere within the sampling area (ranging from 13 to 69 ha [Swetnam 1993]) every five years, averaged over a period of 2000 yr, with considerable variability at the decadal and centennial scales and between groves (Swetnam et al. 1992). These

¹Present address: Elm Road Generating Station, Bechtel Corporation, 11050 South Chicago Road, Oak Creek, WI 53154.

surface fires occurred in a patchy, mosaic pattern, and because crown fires involving *S. giganteum* were evidently rare (judging from the presence of trees in excess of 1500 yr old), caused little mortality to large trees. Frequent, low intensity ground fires were probably important for forest health and maintained *S. giganteum* groves in open, park-like stands.

From about 1860 to 1900, natural ecosystem processes in *S. giganteum* stands, including fire, were drastically altered by livestock grazing (mainly sheep), cessation of aboriginal burning practices, limited logging, and suppression of natural or human-caused wildfires (Kilgore and Taylor 1979). Currently, many mixed conifer forest stands at Calaveras Big Trees State Park are thickets of mid-sized trees, often dominated by *Abies concolor* (Gordon and Glend.) Lindley (white fir) and *Calocedrus decurrens* (Torrey) Florin (incense cedar). There is little understory vegetation because the overstory canopy is almost closed and provides little opportunity for light to reach the forest floor. The conditions wherein *S. giganteum* stands can self-perpetuate and flourish no longer exist.

Based on tree-ring analysis, from 500 AD to 1900 AD, the longest recorded period without a fire in a *S. giganteum* stand was approximately 60 yr, while during centuries with high fire frequencies (generally periods of drought) the longest non-burn interval per stand was typically no more than 13 yr (Swetnam 1993). There are currently some *S. giganteum* stands that have had no fire for the past 100 yr.

Prescribed fire has been introduced into *S. giganteum* stands in many parks in the Sierra Nevada, including Calaveras Big Trees State Park, as a means of restoring more natural conditions. Ground fires have typically been set under proper conditions in late summer or fall with goals of removing excessive fuels, killing invading *A. concolor* and *C. decurrens* trees, and restoring natural processes. Experience at Calaveras Big Trees State Park has revealed that for up to 15 yr following initial prescribed burning, the understory vegetation and overstory canopy conditions will not support extensive surface fires. Maintaining a mean fire return interval of five years has not been possible because not enough fuel is available to adequately carry surface fire throughout *S. giganteum* stands. To approach the relatively short mean fire return interval suggested by the tree-ring fire-scar evidence, it appears there may have been different overstory species, such as deciduous hardwoods, contributing fuel to the forest floor, or understory shrubs, herbs, or grasses that grew more densely and provided fuel for frequent fires.

The precise structure of pre-1850 *S. giganteum* stands, particularly the composition and biomass of understory plant species, is unknown (Vankat

and Major 1978; Stephenson 1996; Stephenson 1999). In the 1860s, livestock grazing, principally large flocks of sheep, was introduced into the central Sierra Nevada (Swetnam 1993; Kilgore and Taylor 1979), suggesting there was a substantial amount of forage available. Researchers in many areas of the western United States, particularly the monsoonal southwest, have found that fine fuels, especially grasses, were important for the spread of ground fires. The removal of these fuels through overgrazing by livestock beginning in the mid-1800s probably led to sharp declines in fire frequency (Swetnam et al. 1991; Caprio and Lineback 2002).

Prior to alteration of natural fire regimes in the mid-1800s, *S. giganteum* and mixed conifer stands in the vicinity of Calaveras Big Trees State Park were probably composed of widely spaced, large diameter, towering *S. giganteum*, a few *Pinus lambertiana* Douglas (sugar pine) and *Pinus ponderosa* Laws. (ponderosa pine), and a lesser element of *A. concolor* and *C. decurrens*. These stands were probably devoid of dense woody understory vegetation because of frequent surface fires ignited by native people or lightning. The open nature of these stands may have allowed sufficient sunlight to reach the forest floor to support an extensive understory of native grass species, which during the dry season served to carry frequent surface fires throughout the forest stand (e.g., Swetnam et al. 1992). These surface fires would have killed most small shrubs and trees, removed smothering duff layers, recycled nutrients, perpetuated the grass-dominated understory vegetation, and maintained gaps in the stands for forest regeneration. Unfortunately, little solid evidence exists either way regarding the existence of this prehistoric grass understory.

We used phytolith analysis to test the hypothesis that grasses were an important prehistoric component of the understory of *S. giganteum* stands. Opal phytoliths are microscopic particles of silica formed in the cells of many plants and released into the soil during decomposition (Piperno 2006). Phytoliths are highly resistant to weathering and in many soil environments will persist for thousands or even millions of years (Wilding 1967; Strömberg 2004). Grasses produce many more phytoliths than most other plant taxa, averaging 3% and commonly ranging from 1–5% dry weight phytolith content (Witty and Knox 1964; Piperno 2006). Most conifer species produce <0.5% dry weight phytolith content (Klein and Geis 1978; Hodson et al. 1997). Consequently, soils formed under grassland vegetation contain an order of magnitude more phytoliths (1–3%) than soils formed under forest vegetation with few grasses (Witty and Knox 1964; Jones and Beavers 1964; Wilding and Drees 1968; Norgren 1973; Miles and Singleton 1975).

Phytoliths often take the shape of the cell in which they are formed. Most phytolith shapes are produced by many different plant taxa, but a few taxa produce distinctive phytolith morphotypes (Rovner 1971). Grasses produce short cell phytoliths in specialized silica accumulator cells that are diagnostic of the Poaceae family. Short cell phytoliths, including rondels, bilobates, and saddles, have been used to identify grasses to the subfamily level (Twiss et al. 1969; Twiss 1992; Mulholland and Rapp 1992).

Several studies have used soil phytoliths to document changes in dominant vegetation over time. In the prairie peninsula in Illinois, Wilding and Drees (1968) used differences in soil phytolith content (measured as percent dry weight) to identify areas of prehistoric forest, grassland, and the forest-grassland ecotone. In Utah, Fisher et al. (1995) used changes in phytolith morphotype percentages in the soil profile to document a shift from grassland to shrubland with the introduction of grazing. Bartolome et al. (1986), working at Jepson Prairie in the California Central Valley, used changes in the concentration of bilobate grass phytolith shapes with soil depth to infer a prehistoric shift from *Nassella*-dominated perennial grassland to the exotic annual grassland present today. Bicknell et al. (1992, 1993) used soil phytolith concentration to map the extent of prehistoric grasslands at several state parks in coastal California, finding many currently forested areas were grasslands prior to European settlement and many current grasslands were previously forested. In northern Arizona, the percent dry weight of phytoliths in the soil and the relative percent of morphotypes in the soil phytolith assemblage were analyzed for a *P. ponderosa* forest with a bunchgrass understory to determine the long-term stability of the current vegetation (Kerns 1999, 2001; Kerns et al. 2001, 2003). High concentrations of pine and grass phytoliths in soil surface and sub-surface samples indicated little change over time. All of these studies have indicated that if there was substantial prehistoric grass cover on a site, there will be a high concentration of grass phytoliths in the soil.

METHODS

Site Description

The study area is located in the South Grove Natural Preserve of Calaveras Big Trees State Park, 200 km east of Stockton, California (Fig. 1). The park is 2625 ha with an elevation range from 1000 m to 1700 m. Topography is dissected, with a western slope overall, and NE-SW trending ridges between steep river canyons. The climate of the western Sierra Nevada is

distinctly seasonal and highly influenced by elevation. The annual precipitation at the elevation of the park ranges from 100 to 170 cm, much of it coming as snow; about 90% of the total precipitation occurs during the six month period between November and April (Walfort and Hunt 1982).

Soils in the South Grove Natural Preserve (Fig. 2) are dominated by the McCarthy series, inceptisols characterized as gravelly sandy loam/very gravelly sandy loam found on slopes of 5 to 60%. Soil pH ranges from 6.3 at the surface to 5.9 at 60 cm depth. Parent material is well-drained, basic, volcanic rock with rapid permeability.

Overstory vegetation at Calaveras Big Trees State Park is largely pine/mixed pine and fir forest dominated by *Pinus ponderosa* (ponderosa pine), *Pinus lambertiana* (sugar pine), and *Abies concolor* (white fir) in either pure or mixed stands. *Calocedrus decurrens* (incense cedar), *Quercus kelloggii* Newb. (California black oak) and *Quercus chrysolepis* Liebm. (canyon live oak) also occur within the park. Vascular plants that have been identified in the park include over 60 families, 159 genera, and 219 species (Walfort and Hunt 1982). Common species are listed in Table 1.

The *Sequoiadendron giganteum* (giant sequoia) stands of the park are located in two groves, designated the North and South Groves. In the never-logged South Grove, *S. giganteum* comprises 65.9% of the total basal area, followed by *A. concolor* at 21.7% (Walfort and Hunt 1982). Grass cover is very sparse throughout the grove, with maximum 5% cover in patches near the top of the watershed's north ridge.

Phytolith Reference Collection

To better understand the soil phytolith assemblage, a phytolith reference collection, composed of phytoliths extracted from leaf samples from all major plant species currently present in the study area (Table 1), was assembled. Phytoliths were extracted using a modified dry ashing technique (Piperno 2006; Pearsall 2000; Kondo et al. 1994). Samples were washed in distilled water to remove adhering minerals, dried at 60 C and weighed, rinsed in 10% HCl to improve combustion, ashed in a muffle furnace at 550 C for 4 hr, rinsed again in 10% HCl to remove acid-soluble residue, washed 3 times in water, dried in ethanol, and the dry residue weighed. To view phytoliths, dry residue was resuspended in immersion oil so that phytoliths could be rotated and three-dimensional characteristics observed, mounted on a slide, and viewed under a phase-contrast light microscope at 400 \times . Two slides for each plant were scanned completely and potentially diagnostic phytolith types noted.

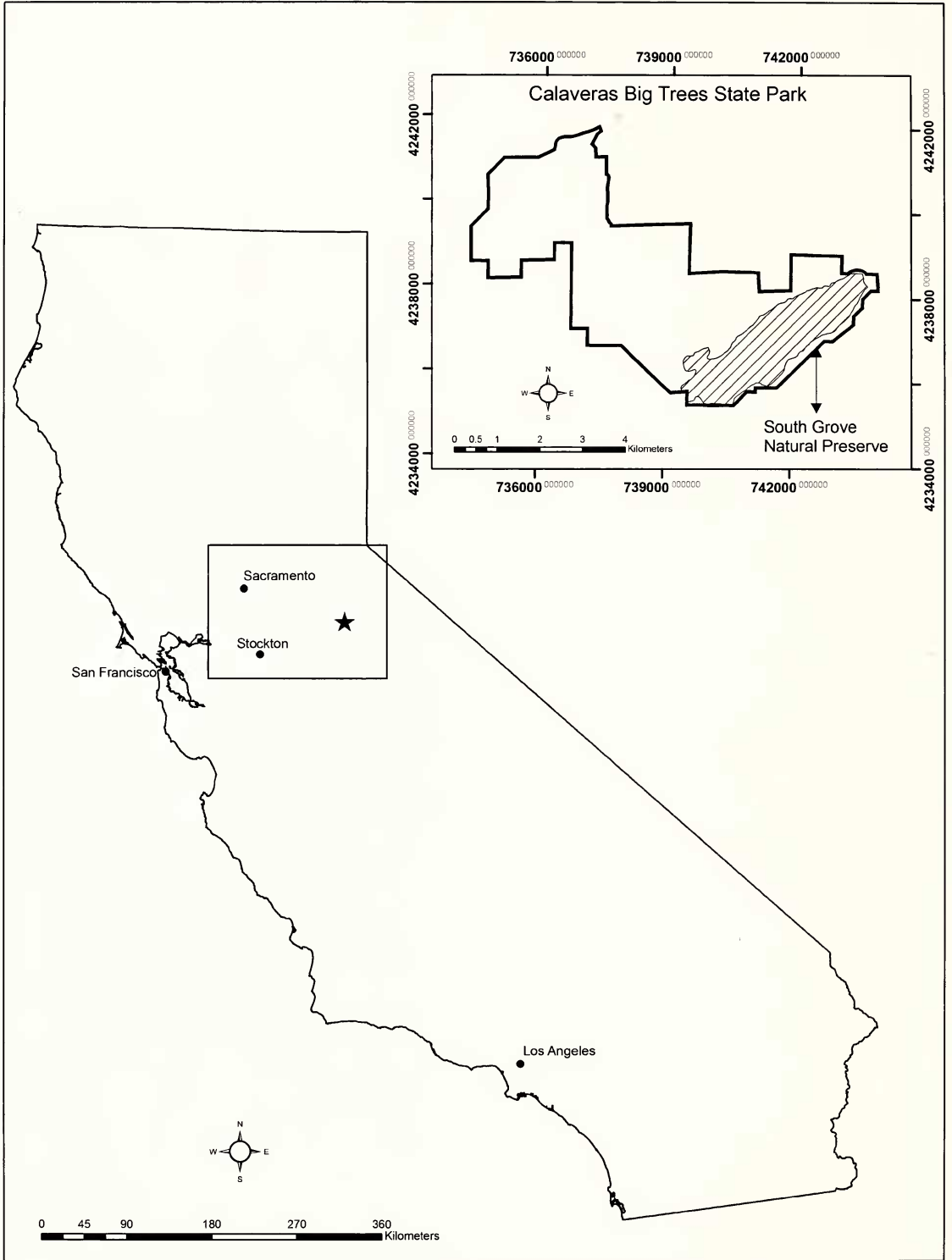


FIG. 1. Location of Calaveras Big Trees State Park and the South Grove Natural Preserve, georeferenced in UTM.

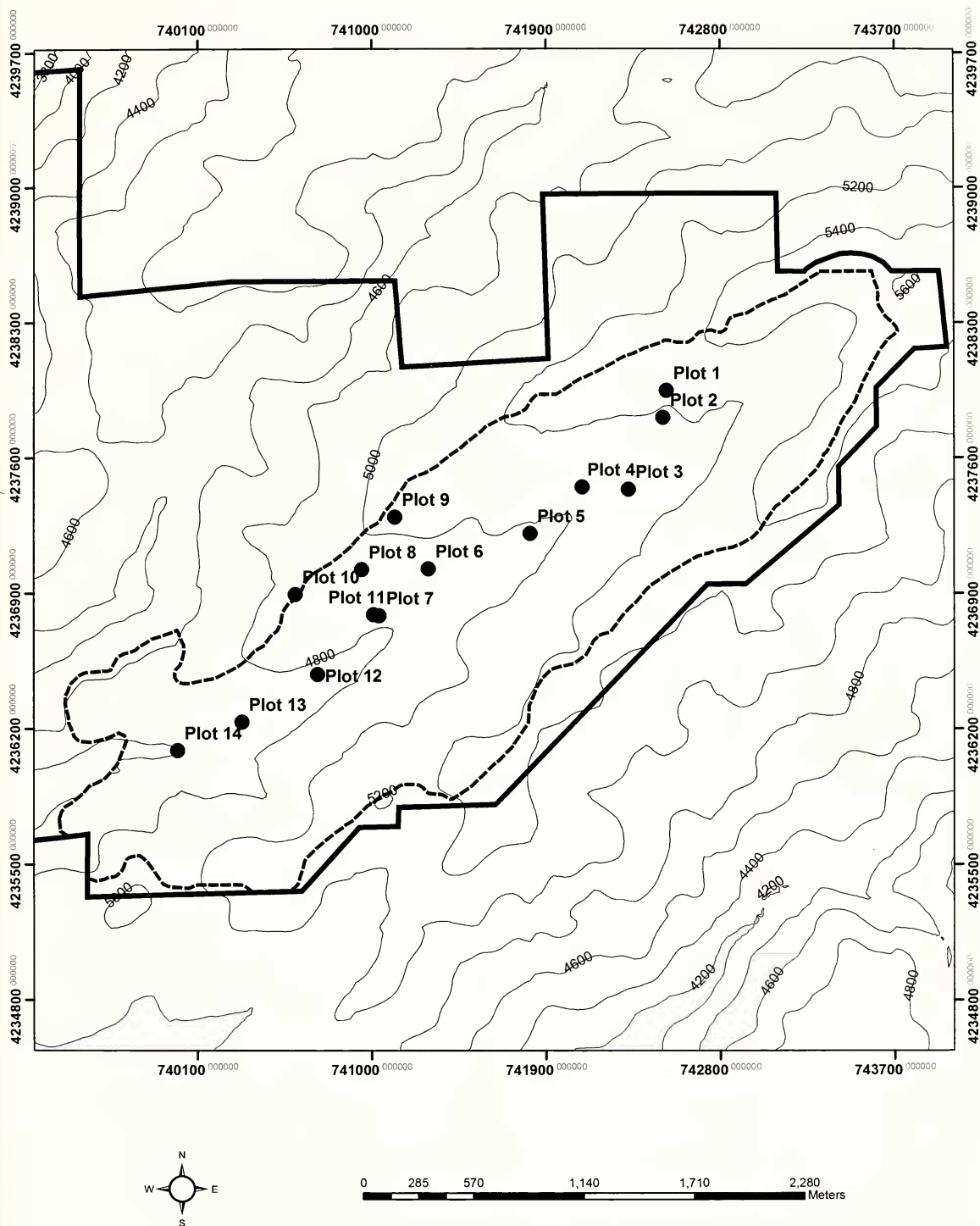


FIG. 2. Location of phytolith sampling plots in the South Grove Natural Preserve, Calaveras Big Trees State Park, georeferenced in UTM.

Soil Phytolith Extraction

Soil samples were collected from soil pits dug on 14 plots (Fig. 2). Plots were selected to span the topographic gradient of the watershed,

particularly but not exclusively in locations currently occupied by giant sequoia. To assess within plot variation in soil phytoliths, two pits within 100 m of each other were dug and sampled at each plot. Phytolith samples from both pits

TABLE 1. PLANT SPECIES PRESENT IN CALAVERAS BIG TREES STATE PARK, SAMPLED FOR THE PHYTOLITH REFERENCE COLLECTION, WITH LEAF SILICA PERCENTAGE BY WEIGHT AND OBSERVED DIAGNOSTIC PHYTOLITH MORPHOTYPES.

Species	Family	Common Name	Silica (%)	Diagnostic Morphotypes
Trees				
<i>Abies concolor</i> (Gordon and Glend.) Lindley	Pinaceae	white fir	0.1	none
<i>Acer macrorhyllum</i> Pursh	Aceraceae	big-leaf maple	0.5	none
<i>Alnus rhombifolia</i> Nutt.	Betulaceae	white alder	<0.1	none
<i>Calocedrus decurrens</i> (Torrey) Florin	Cupressaceae	incense cedar	<0.1	none
<i>Cornus nuttallii</i> Audubon	Cornaceae	dogwood	<0.1	none
<i>Corylus cornuta</i> Marsh var. <i>californica</i> (A. DC.) W. Sharp	Betulaceae	California hazelnut	0.3	none
<i>Pinus lambertiana</i> Douglas	Pinaceae	sugar pine	<0.1	none
<i>Pinus ponderosa</i> Laws.	Pinaceae	ponderosa pine	0.5	spiny bodies, spiny rods
<i>Pseudotsuga menziesii</i> (Mirbel) Franco var. <i>menziesii</i>	Pinaceae	Douglas-fir	0.4	none
<i>Quercus kelloggii</i> Newb.	Fagaceae	black oak	0.3	none
<i>Sequoiadendron giganteum</i> (Lindley) Buchholz	Taxodiaceae	giant sequoia	0.1	none
Shrubs				
<i>Arctostaphylos patula</i> Greene	Ericaceae	green-leaf manzanita	<0.1	none
<i>Ceanothus cordulatus</i> Kellogg	Rhamnaceae	mountain whitethorn	0.6	none
<i>Ceanothus integerrimus</i> Hook. & Arn.	Rhamnaceae	deer brush	<0.1	none
<i>Chamaebatia foliolosa</i> Benth.	Rosaceae	mountain misery	0.4	none
<i>Chimaphila umbellata</i> (L.) Bartram	Ericaceae	pipsissewa	0.1	none
<i>Chrysolepis sempervirens</i> (Kellogg) Hjelmq.	Fagaceae	bush chinquapin	0.1	none
<i>Rhododendron occidentale</i> (Torrey & A. Gray) A. Gray	Ericaceae	western azalea	<0.1	none
<i>Rosa pinetorum</i> A.A. Heller	Rosaceae	pine rose	0.4	none
<i>Rubus parviflorus</i> Nutt.	Rosaceae	thimbleberry	<0.1	none
<i>Ribes roezlii</i> Regel	Grossulariaceae	Sierra gooseberry	0.2	none
<i>Symphoricarpos mollis</i> Nutt.	Caprifoliaceae	snowberry	<0.1	none
Herbs				
<i>Adenocaulon bicolor</i> Hook.	Asteraceae	trail plant	0.1	none
<i>Aquilegia formosa</i> Fischer	Ranunculaceae	crimson columbine	0.1	none
<i>Asarum hartwegii</i> S. Watson	Aristolochiaceae	wild-ginger	<0.1	none
<i>Carex</i> sp.	Cyperaceae	sedge	4.3	conical cells
<i>Clintonia uniflora</i> (Schultes) Kunth	Liliaceae	bride's bonnet	<0.1	none
<i>Fragaria vesca</i> L.	Rosaceae	wood strawberry	0.2	none
<i>Galium aparine</i> L.	Rubiaceae	goose grass	2.3	none
<i>Hieracium albiflorum</i> Hook.	Asteraceae	hawkweed	0.2	none
<i>Iris hartwegii</i> Baker	Iridaceae	Hartweg's iris	0.2	none
<i>Lonicera involucrata</i> (Richardson) Banks	Caprifoliaceae	twiberry	<0.1	none
<i>Lupinus</i> sp.	Fabaceae	lupine	0.1	none
<i>Phacelia</i> sp.	Hydrophyllaceae	phacelia	0.3	none
<i>Pyrola picta</i> Smith	Ericaceae	white-veined shinleaf	0.1	none
<i>Smilacina racemosa</i> (L.) Link	Liliaceae	false solomon's seal	<0.1	none
<i>Trientalis latifolia</i> Hook.	Primulaceae	starflower	<0.1	none
<i>Viola lobata</i> Benth.	Violaceae	pine violet	<0.1	none
Grasses				short cells, trichomes, bulliforms
<i>Achnatherum lemmonii</i> (Vasey) Barkworth	Poaceae	Lemmon's stipa	5.1	bilobate short cells
<i>Bromus carinatus</i> Hook. & Arn.	Poaceae	California brome	4.5	rondel short cells
<i>Danthonia unispicata</i> (Thurber) Macoun	Poaceae	one-spike oatgrass	1.9	bilobate short cells
<i>Elymus elymoides</i> (Raf.) Swezey	Poaceae	squirreltail	13.5	rondel short cells
<i>Festuca rubra</i> L.	Poaceae	red fescue	3.4	rondel short cells
<i>Melica aristata</i> Bolander	Poaceae	awned melic	3.2	bilobate short cells
<i>Poa secunda</i> J.S. Presl	Poaceae	one-sided bluegrass	6.1	rondel short cells

TABLE 2. SOIL PHYTOLITH WEIGHT AS A PERCENTAGE OF SOIL WEIGHT AND PERCENTAGE OF DIAGNOSTIC GRASS PHYTOLITHS IN SOIL PHYTOLITH ASSEMBLAGE IN RELATION TO SOIL DEPTH AND TOPOGRAPHIC POSITION IN THE SOUTH GROVE NATURAL PRESERVE, CALAVERAS BIG TREES STATE PARK.

Topographic Position	Soil Depth (cm)	Soil Phytolith Weight (%)	95% t-value Confidence Interval	Grass Phytoliths (%)	95% t-value Confidence Interval
Hillside plots (N=9)	Surface	0.08	0.06–0.10	21	14–28
	10	0.04	0.03–0.05	17	12–22
	25	0.02	0.01–0.03	26	17–35
	40	<0.01	—	—	—
	55	<0.01	—	—	—
Ridge-top PIPO plots (N=6)	Surface	0.47	0.35–0.59	12	5–19
	10	0.36	0.24–0.48	12	10–14
	25	0.37	0.25–0.49	15	10–20
	40	0.32	0.15–0.49	11	1–21
	55	0.18	0.00–0.38	15	8–22
Lower channel-side plots (N=4)	Surface	0.31	0.25–0.37	43	37–49
	10	0.52	0.38–0.66	31	20–42
	25	0.53	0.39–0.67	38	30–46
	40	0.44	0.33–0.55	35	18–52
	55	0.43	0.35–0.51	42	28–56

were processed and counted for plots that had >0.10% soil phytoliths; otherwise, samples from only one pit were processed. Soil samples were collected from each pit at five depths, each depth corresponding to a soil horizon because soils were similar throughout the site: mineral soil surface (A horizon), 10 cm (upper B horizon), 25 cm (middle B horizon), 40 cm (lower B horizon), and 55 cm (C horizon). Because the soil horizon generally corresponded with soil depth, soil phytolith data from each plot were aggregated by sample depth, which may be a rough approximation of relative sample age (e.g., Alexandre et al. 1999), for analysis.

Phytoliths were extracted from five gram soil samples by standard procedures: deflocculation in Calgon, HCl wash, organic matter digestion in 30% hydrogen peroxide, two heavy liquid flotations in zinc bromide solution at specific gravity 2.30 (a third flotation for several samples produced negligible additional phytoliths and was deemed unnecessary), and mounted on slides as above (Carbone 1977; Kondo et al. 1994). Because the biogenic silica residue contained diatoms and residual mineral silica particles, phytolith weight for each sample was estimated by examining 10 microscope fields on a slide, estimating the percentage of non-phytolith material, and subtracting this percentage from the measured residue weight (Carnelli et al. 2001). Phytolith morphological types were tallied for each soil sample until 400 total phytoliths were counted. Diagnostic types were tallied individually by taxon. Non-diagnostic types were lumped together; no attempt was made to identify or tally each individual non-diagnostic type. The percentage of diagnostic grass phytoliths (i.e., morphotypes observed in grasses but not observed in

other plants in the reference collection, including simple trichomes, bulliforms, three types of long cells, and short cells) out of total phytoliths in each sample was calculated.

RESULTS

Extracted reference material from most plant species contained small amounts of poorly silicified biogenic silica but no diagnostic phytoliths (Table 1). *Pinus ponderosa* was the only tree species with diagnostic phytoliths: spiny bodies and spiny rods (Norgren 1973; Kerns 2001) were isolated from needles. Several tree species produced phytolith morphotypes that were distinct from grasses but not diagnostic beyond this level. No shrubs contained diagnostic phytoliths. *Carex* (sedge) species produced non-diagnostic long cells and diagnostic conical phytoliths (Ollendorf 1992). All grasses contained abundant phytoliths, including long cells, trichomes, bulliforms, and short cells (Twiss et al. 1969; Twiss 1992). *Achnatherum lemmonii* (Vasey) Barkworth, *Danthonia unispicata* (Thurber) Macoun, and *Melica aristata* Bolander were the only grasses sampled producing bilobate short cells. Other grasses produced abundant rondel short cells.

Soil phytolith weight averaged less than 0.55% on all plots (Table 2), but varied according to topographic position in the watershed. Hillside plots (Fig. 2: Plots 1–7, 11, 12), typical of most of the sampled watershed, had very low soil phytolith concentration (<0.10%) at all depths. Plots on or near the ridge (Plots 8–10), where *P. ponderosa* was present in the overstory, contained significantly more soil phytoliths (of which 42% were *P. ponderosa* spiny bodies) at all depths than hillside plots. Plots in the lower part of the

TABLE 3. ESTIMATED PERCENTAGE OF PHYTOLITHS IN THE SOIL BENEATH GRASSLAND AND FOREST VEGETATION FROM STUDY SITES IN NORTH AMERICA.

Location	Vegetation Type	Soil Phytolith (%)	Size Fraction (μ)	Estimation Method	Reference
Alberta	Grassland	0.83–2.78	20–50	particle count	Lutwick and Johnston 1969
Arizona	Ponderosa pine-grassland	0.9–1.4	5–250	dry weight	Kerns et al. 2001
Illinois	Grassland	0.77–1.23	20–50	particle count	Beavers and Stephen 1958
	Hardwood forest	0.19–0.28	20–50	particle count	Beavers and Stephen 1958
Minnesota	Oak forest and grassland	1.54–3.63	5–50	particle count	Verma and Rust 1969
North Carolina	Oak hardwood and grass	0.94–0.99	all	dry weight	Knoepp et al. 1998
Oregon	Ponderosa pine	0.13–0.26	15–100	particle count	Witty and Knox 1964
	Grassland	1.92–2.89	15–100	particle count	Witty and Knox 1964
Pennsylvania	Grassland	1.19–1.75	20–50	dry weight	Waltman and Ciolkosz 1995
	Hardwood forest	0.07–0.33	20–50	dry weight	Waltman and Ciolkosz 1995

watershed within <50 m of the stream channel (Plots 13, 14), where no *P. ponderosa* was observed in the overstory, also contained significantly more soil phytoliths than hillside plots.

All plots contained diagnostic grass phytoliths, but topographic position influenced grass phytolith percentages (Table 2). Hillside plots had the lowest percentage of grass phytoliths; channel-side plots had significantly more grass phytoliths than either of the other topographic positions. The dominant morphotypes comprising the grass phytolith percentage were rondel short cells and several types of elongate cells observed only in grasses in the reference collection. Extremely few bilobate phytoliths (<0.1% on all plots) were found, indicating none of the bilobate-producing grasses, *A. lemmonii*, *D. unispicata*, and *M. aristata*, had significant prehistoric cover on any of the plots. All ridge-top plots had >10% *P. ponderosa* spiny bodies and spiny rods throughout the soil profile, indicating long-term presence of this species there. All plots contained substantial percentages of non-diagnostic phytoliths, dominated by several non-diagnostic types of elongate cells, but also including blocky polyhedrals, tracheary elements, epidermal cells, mesophyll cells, and hair cells (Piperno 2006). Although non-diagnostic phytoliths were counted, they were not quantitatively categorized because the reference material suggested these types would not provide useful information due to considerable redundancy between species. However, there were few obvious differences in the assemblage composition of non-diagnostic phytoliths in relation to soil depth or between plots. Many of these non-diagnostic morphotypes may have been produced by grasses.

DISCUSSION

The lack of diagnostic phytoliths in most of the reference material was in agreement with other studies of similar species. The only surprising

result was the *Pseudotsuga menziesii* (Mirbel) Franco var. *menziesii* (Douglas-fir) sample contained no diagnostic asterosclereid phytoliths observed by several others (Brydon et al. 1963; Norgren 1973; Blinnikov 2005). One explanation (although there is no supporting mineralogical data available) is that if the soils on the site are rich in aluminum and/or iron oxides, silica in solution available to plants for phytolith formation may be reduced considerably (Beckwith and Reeve 1963; Jones and Handreck 1965). Other plausible explanations are the needles collected were too young to have much silicification or the asterosclereids may have been present but damaged in processing, broken into pieces that were unrecognizable.

Grassland soils have been found by various researchers to contain at least 5–10 times more phytoliths by weight than forest soils, which generally have phytolith content between 0.1 and 0.5% by weight (Table 3). A site in the *P. ponderosa*-bunchgrass vegetation type in northern Arizona (7–50% grass cover in the understorey), probably the closest phytolith analog for Sierra Nevada mixed conifer forests if they had a prehistoric grass understorey, showed total phytolith content of 1–1.4% (Kerns 1999; Kerns et al. 2001). Grass phytoliths made up approximately half of the total, *P. ponderosa* the other half (B. Kerns personal communication).

Phytolith concentration on hillside plots in our study was at the low end of published data, even for forest plots. The paucity of phytoliths observed in most plant reference material species (Table 1) suggests that very few phytoliths would be deposited in the soil unless substantial cover of heavy phytolith producing plants not present on the plots today (*P. ponderosa*, grasses, or sedges) were present on the plot for a substantial period of time in the past.

Ridge-top plots had phytolith concentrations within the expected range for forest soils, but considerably less than found at the *P. ponderosa*-

bunchgrass site in northern Arizona. *Pinus ponderosa* and bunchgrasses are currently minor components of the vegetation on these plots; grasses (mostly *Bromus carinatus* Hook. & Arn. and *Elymus elymoides* (Raf.) Swezey) are present with <5% cover. The phytolith evidence suggests that *P. ponderosa* and bunchgrasses were prehistorically present but have remained minor components of ridge-top vegetation.

Lower channel-side plots had higher grass phytolith concentration than expected for forest soils, but less than half the concentration typical of grassland. There are currently very few grasses in this part of the watershed. One possible explanation is that there was a prehistoric stringer meadow associated with the stream that disappeared when the water table dropped due to down-cutting. This interpretation is supported by data from phytolith sampling of a small stringer meadow in the mixed-conifer forest in the Sierra San Pedro Martir in Baja California, that had total phytolith weight and percentage of grass phytoliths comparable to these plots (R. Evett et al. In Press).

Phytolith migration and dissolution, alternative explanations for low soil phytolith weights, must be ruled out before the grass understory hypothesis can be rejected. Because they are mostly silt-sized particles, phytoliths are known to migrate downward in the soil profile, particularly in sandy soils (Starna and Kane 1983). Sampling at several depths in soil pits revealed no evidence of substantially fewer phytoliths at the surface or accumulation of phytoliths at any depth (Table 2). Phytolith degradation and dissolution is known to occur under alkaline soil conditions but only under the most severe acidic conditions (Piperno 2006). The soil type sampled, the McCarthy series, is slightly acidic (pH 6.3–6.4) (Walfort and Hunt 1982), which provides ideal conditions for soil phytolith preservation. Phytolith migration and dissolution are not plausible explanations for the lack of grass phytoliths in South Grove soils.

In the absence of phytolith migration, it is reasonable to expect increasing phytolith age and decreasing phytolith concentration with increasing soil depth (Alexandre et al. 1999; Piperno 2006). Although no dating was attempted (and would be difficult to interpret because of bioturbation issues), phytoliths from each sampled soil profile probably span at least the past 1500 yr, the age of the oldest living *S. giganteum* in the stand, but more likely several thousand years.

The phytolith evidence indicates that grasses, while certainly present, have not been a major component of the *S. giganteum* forest understory in the South Grove Natural Preserve. We conclude that grass was not likely to have been present with enough cover to be a major source

of fine fuel required to carry frequent prehistoric ground fires in this *S. giganteum* stand. Because none of the other plant species examined (except for sedges and *P. ponderosa*) produced diagnostic phytoliths, the prehistoric presence of deciduous trees, shrubs, or other herbaceous species in the understory could not be determined from phytolith evidence. There is the possibility that more detailed work, beyond the scope of this study, analyzing many more samples of reference material from other sites, could identify more diagnostic phytoliths and signature phytolith assemblages to shed more light on the presence of prehistoric understory species.

Other research supports the conclusion that grass was not a substantial component of the giant sequoia forest understory. For example, even under the high levels of light that exist after logging, Biswell et al. (1966a) found that grass-like plants had less than 10% frequency in giant sequoia forests. Phytolith data from a relatively open, mixed conifer forest in the Sierra San Pedro Martir, Mexico, suggest that grasses may not have been a major component of the understory (R. Evett et al. In Press).

Parsons (1978) found at Redwood Mountain (approximately 100 km south of Calaveras Big Trees State Park and 550 m higher elevation) that forest floor fuel loads following the first prescribed fire in a *S. giganteum* stand were similar to unburned stands 7 yr following burning; however, he attributed much of this fuel to material killed by the prescribed fire from *A. concolor* that had invaded the giant sequoia stands during the past 100 yr when fire was absent. Parsons predicted that a second prescribed fire would remove this fuel source; it was unclear where additional fuel to support a short fire interval would come from. This is in contrast to data from (Biswell 1966b), who found that *S. giganteum* stands produced large amounts of litter each year, ~9000 lbs/acre.

It is possible that deciduous hardwoods co-occurring with *S. giganteum* provided sufficient surface fuels prior to the mid-1800's to achieve an average five year fire interval. As a result of livestock grazing and the altered fire situation for the past 150 yr, hardwoods such as *Quercus kelloggii* (black oak) are now uncommon in *S. giganteum* stands (Biswell et al. 1966a; Bonnicksen and Stone 1982). Further research is necessary to investigate the possibility of hardwoods as a fuel source.

Parsons (1995) stated that fire in giant sequoia stands stimulated shrub and hardwood growth. The patchy nature of natural fires, with irregular shapes and varying rate of spread, and role of occasional intense fires (Stephenson et al. 1991) provides opportunity for shrubs to provide a significant amount of fuel. Common shrubs in the vicinity of giant sequoia stands include

Chamaebatia foliolosa Benth. (mountain misery), *Ceanothus cuneatus* (Hook.) Nutt. (buckbrush), *Ceanothus integerrimus* Hook. & Arn. (deerbrush), and *Chrysolepis sempervirens* (Kellogg) Hjelmq. (bush chinquapin). Of these, *C. foliolosa* seldom occurs in *S. giganteum* stands and would be displaced by frequent burning. *Ceanothus* species are known to invade areas following disturbance but have never been commonly found within *S. giganteum* stands. *C. sempervirens* burns well but is typically only dense on north-facing slopes. Because phytolith analysis provides no information on these shrubs, resolving the question of their abundance in *S. giganteum* stands remains problematic. *Ceanothus cordulatus* Kellogg and *Chamaebatia foliolosa*, although lacking in diagnostic phytoliths, produce enough biogenic silica (Table 1) to contribute considerable quantities of phytoliths to the soil. Further study of their phytolith assemblages in reference material may eventually produce a soil phytolith assemblage signature for these two shrubs.

There also are several alternative explanations, not requiring post-European settlement changes in the forest understory, which could account for the lack of success achieving fire return intervals approaching five years with prescribed burning at the South Grove Natural Preserve. The simplest explanation is the five year estimate is based on a composite of 2000 yr of tree-ring fire-scar data from five *S. giganteum* groves along a 160 km transect in the Sierra Nevada, with substantial variation between groves and substantial variation at decadal and centennial scales correlated with fluctuating climate (Swetnam 1993). The South Grove Natural Preserve is further north than any of the sampled groves and may be more mesic, while the current climate of the region may also be more mesic than average (Cook et al. 2004, Grid 47), leading to a longer than average expected fire return interval. Also, if very small fires (recorded by only a single tree) are excluded, the mean fire return interval for three of the five *S. giganteum* groves sampled is close to 10 yr (Swetnam et al. 1992).

Miller and Urban (1999), based on a model of the surface fire regime in mid-elevation coniferous forests of the Sierra Nevada, suggested the fire return interval depends on forest floor fuel load and fuel moisture. Their model indicated that even without a grass understory, there may be sufficient fuel accumulation on the forest floor to support a five year or less fire return interval under conditions of very low (<5%) fuel moisture (Miller and Urban 2000). Their simulations showed that under average climate conditions, with no grasses or shrubs in the understory, the mean fire return interval at the elevation of the South Grove Natural Preserve should be ~6 yr

(Miller and Urban 1999). According to the model, a five year accumulation of *S. giganteum* litter should be enough to carry at least a patchy fire, but perhaps only under more extreme weather conditions (low humidity, high temperature, high wind) that are not always accompanied by an ignition source. Many of the fires seen in the tree-ring fire-scar record may have been intentionally set by humans whenever extreme conditions were present, without concern for catastrophic fires because they knew the intensity would be very low. Because of safety concerns, prescribed burning typically occurs during periods with higher levels of fuel moisture when effective fuel connectivity is much lower. Because considerably more fuel accumulation is required to carry an extensive prescribed fire, a longer fire return interval would be expected.

Given the short prehistoric fire return interval and more widely spaced trees, litter build-up was probably very uneven on the forest floor, leading to highly patchy, low intensity fires. This has been observed in mixed conifer forests in the Sierra San Pedro Martir, where forest structure remains relatively open because of a continuing fire regime (Stephens et al. 2003). The mean fire return interval, based on the frequency of occurrence of all fires on a sampled site, may be misleading if there are frequent, small fires that burn very little area; burning every part of the stand may take considerably longer. A 25% composite mean fire return interval, calculated from fires scarring >25% of the recording trees in a stand, may be more useful to estimate the frequency of widespread fires in a highly patchy environment (Dieterich 1980; Swetnam and Baisan 2003). Another better measure in this patchy situation may be the fire rotation period, defined as the average length of time between fires averaged for each fire-scar recording tree (Baker and Ehle 2001). This gives an estimate of the maximum time required to burn an area the size of the stand, and may more accurately represent temporal burning patterns in *S. giganteum* stands. Expecting a prescribed fire to burn through an entire stand every five years is probably unrealistic. Mean fire return intervals estimated using the 25% filter or fire rotation period would be considerably longer than five years and probably more indicative of the time required to burn the entire stand. The currently observed 15–20 yr period required for enough fuel to accumulate between prescribed fires given the present climate may be representative of the fire regime under a similar climate in the past.

The management goal for Calaveras Big Trees State Park is to ensure natural processes are the principal influence on *S. giganteum* stands so that large, exceptional specimens can grow to maturity and the species can regenerate naturally. Current forest conditions, because of past logging

and fire suppression, have created an environment wherein *S. giganteum* does not regenerate naturally because of a lack of surface fire, and large mature trees are at risk from catastrophic crown fires carried by the tightly crowded thickets of fir and pine trees that have developed in the absence of surface fires. Through phytolith analysis, an inexpensive approach to definitively test for the presence of prehistoric grass, we have shown that the prehistoric frequent fire regime at South Grove Natural Preserve probably did not depend on a grass understory. Grass should probably not be a major part of management strategies seeking to mimic prehistoric fire regimes. The South Grove is typical of other stands of *S. giganteum* in the central Sierra Nevada. The results of this study, if replicated at other locations, may be applicable to *S. giganteum* fire management in a much wider region.

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